



Weak fine-scale genetic structure and considerable life-history diversity in a near-pristine subarctic Atlantic salmon (*Salmo salar*) river

María I. Cádiz¹ · Marion Sinclair-Waters^{1,2} · Jaakko Erkinaro³ · Panu Orell³ · Ana S. Lindeza¹ · Morgane Frapin¹ · Amaia Lamarins¹ · Victoria L. Pritchard^{1,4} · Craig R. Primmer¹

Received: 4 February 2025 / Accepted: 1 July 2025 / Published online: 20 August 2025
© The Author(s) 2025

Abstract

The Näätämö River, in the far north of Europe, hosts a large Atlantic salmon (*Salmo salar*) stock with high socio-economic value. The catchment has near-pristine environmental conditions, although there are recent signs of stock declines. It nevertheless offers a good opportunity to monitor the status of a near pristine wild salmon system. This study aimed to characterize the fine-scale genetic structure of Atlantic salmon in the Näätämö River and evaluated the possibility to assign individuals to their population of origin. We genotyped juveniles sampled from eight locations using a 60 K single nucleotide polymorphism (SNP) panel to characterize within-river genetic diversity and structure. We also tested the performance of a previously designed 180 SNP panel to assign individuals to their population of origin. The genetic structure of the Näätämö River salmon population appears weak (F_{ST} ranging from 0.001–0.035), possibly due to natural straying. The performance of the predesigned panel in assigning individuals to their population of origin was moderate to high (82–85%), but customization could further enhance its accuracy. Additionally, we described the life-history diversity of salmon within the river using a long-term scale archive of c. 22,000 individuals collected over 48 years, identifying 59 unique life-history strategies. We suggest that to protect the self-sustaining salmon population in the Näätämö River, it would be important to manage the salmon fishery and conserve the population by incorporating up-to-date knowledge of stock status, considering their genetic structure, substantial gene flow and diverse life history.

Keywords Genetic diversity and structure · Life-history strategies · Conservation · *Salmo salar*

Introduction

Intraspecific variation, including genetic and phenotypic diversity within and among populations, is an essential component of biodiversity, and its dynamics over time and space can influence the fate of a population (Mimura et al. 2017; Des Roches et al. 2018, 2021; Shaw et al. 2025).

Genetic diversity provides the raw material for evolutionary processes (Laikre et al. 2020; Hoban et al. 2020), enhancing organisms ability to adapt to changing environmental conditions and thereby contributing to the long-term survival of species (Agashe 2009; Laikre et al. 2020; Hvilson et al. 2022). Phenotypic variation, particularly in life-history strategies (e.g., age at maturity, migration time and time spent in sea vs. freshwater) enhances resilience through the portfolio effect (Schindler et al. 2010), enabling populations to resist or quickly recover from environmental perturbations by spreading risk temporally and spatially (Pelletier et al. 2020). Human-driven pressures (e.g., harvest, landscape change, climate change, pollution and introduction of predator/prey/host/competitor) are reshaping variation within species by driving rapid evolutionary changes and extirpation of wild populations across freshwater, marine, and terrestrial ecosystems worldwide (Palkovacs et al. 2012). Recent studies have shown that since the Industrial Revolution, the genetic diversity within wild populations

✉ María I. Cádiz
maria.cadiz-escobar@helsinki.fi

¹ Organismal and Evolutionary Biology Research Programme, Faculty of Biology & Environmental Sciences, University of Helsinki, Helsinki, Finland

² UMR AGAP Institut, Univ Montpellier, CIRAD, INRAE, Institut Agro, Montpellier, France

³ Natural Resources Institute Finland (LUKE), Oulu, Finland

⁴ Institute for Biodiversity & Freshwater Conservation, UHI Inverness, Inverness, UK

has declined by nearly 6% (Leigh et al. 2019). Despite its ecological and evolutionary importance and growing threat due to human activities, intraspecific diversity remains under-assessed by global surveys (Laikre et al. 2020). There is, therefore, an increasing need to better understand and quantify intraspecific diversity, which can facilitate effective conservation and management strategies for wild populations (Des Roches et al. 2021), especially those subjected to harvesting.

Genomic tools in conservation allows quick assessment of intraspecific genetic variation (Leigh et al. 2019). Assessing key genetic variation parameters (e.g., heterozygosity, number of alleles, population divergence and gene flow, among others) (Mimura et al. 2017) provides essential information to monitor population status and contribute to management plans. Understanding the extent of the genetic structure has implications for conservation and management (Primmer et al. 2006). For example, the genetic structure of Atlantic salmon populations has been found to vary considerably, going from systems with no structure at all, such as Miramichi River (Wellband et al. 2019), to complex structured systems within a single river, as observed in the Teno River (Vähä et al. 2017), each requiring distinct management considerations. Genetic stock identification (GSI) is a tool that contributes to the conservation and management of fisheries by providing valuable insights into the stock composition and origins of populations (Ensing et al. 2013; Hess et al. 2011; Vähä et al. 2017; Svenning et al. 2019). In addition, the application of GSI has extended to help as a forensic tool to identify illegal harvesting (Nielsen et al. 2012), determine the source of escaped salmon (Glover et al. 2008), and reveal instances of fishing competition fraud (Primmer et al. 2000).

Atlantic Salmon (*Salmo salar*) is an iteroparous fish with ecological, cultural, and economic importance across its range. This species exhibits diverse life-history strategies (Erkinaro et al. 2019), which vary in the time spent in freshwater and the duration of marine migration associated with returning to spawning. Anadromous Atlantic salmon typically spend 1–3 years in freshwater (1–3 RA; river or smolt age) in the south of their range (Klemetsen et al. 2003) and 3–5 years in the north (Niemelä et al. 2006). This is followed by a marine feeding migration where the majority of growth occurs, followed by return migration to fresh water, often homing back to their birth river, mostly one to three years later to spawn (1-3SW; age at maturity, sea age, or number of sea winters) (Klemetsen et al. 2003). Moreover, further life-history strategy diversity is added via iteroparity, i.e., individuals that survive to spawn in several years (Niemelä et al. 2006; Persson et al. 2023).

Globally, Atlantic salmon populations have faced decline or already been extirpated over the past two centuries

(Parrish et al. 1998; Dadswell et al. 2022; ICES 2025). This decline is mainly due to human-related activities, including overfishing, hydropower dams, diseases, pollution, and climate change (Parrish et al. 1998). Additionally, studies have shown shifts in phenotypic traits as age at maturity and growth patterns across their European distribution (Otero et al. 2012; Erkinaro et al. 2019; Harvey et al. 2021; Vollset et al. 2022). Along the northern edge of the species distribution, the salmon stock in the sub-Artic Näätamö River in Fennoscandian North remains one of the relatively large and viable wild populations (Niemelä et al. 2004). While earlier studies reported no consistent decline in their overall abundance from 1975 to 2003 (Niemelä et al. 2004), more recent data show a significant decreasing trend in salmon stocks of the Näätamö River (Kytökorpi et al. 2024), consistent with trends observed in other northern rivers (VRL 2024). Specifically, from 2019 to 2023, the average number of salmon observed has halved compared to previous years (Kytökorpi et al. 2024). Several earlier population genetic studies have included the Näätamö River for comparison to other wild populations (Elo 1993; Elo et al. 1994; Skaala et al. 1998; Asplund et al. 2004; Vähä et al. 2008; Ozerov et al. 2023) and aquaculture origin (Skaala et al. 2004, 2005; Andreassen et al. 2008; Besnier et al. 2011; Glover et al. 2013; Pritchard et al. 2015). However, no study has been conducted on within-river genetic variation and the genetic structure of the salmon in this river.

To address this knowledge gap, we explore fine-scale population genetic structure across the Näätamö River using contemporary genomic data. Juveniles from eight locations were genotyped using a 60 K single nucleotide polymorphism (SNP) panel to assess the genetic diversity and structure. To place our findings in a broader regional context, we compared them with the genetic structure of the nearby Teno River, a well-studied system known for highly structured population complex and life-history variation (Vähä et al. 2007, 2008, 2017; Aykanat et al. 2015; Erkinaro et al. 2019). To evaluate the utility of existing tools for conservation management, we tested the assignment accuracy of a previously designed 180 SNP panel. Additionally, we describe the life-history variation (i.e., quantified the combination of number of years spent in the river as a juvenile, number of years spent feeding at sea, and number of spawning attempts) using a long-term scale archive of c. 22,000 scales collected over 48 years. This study aims to inform evidence-based conservation and bilateral management in a relatively pristine but declining northern salmon system. Specifically, we tested whether (i) fine-scale population genetic structure exists despite minimal anthropogenic impact; (ii) a predesigned 180-SNP panel can accurately assign individuals to origin locations within the river and (iii) the Näätamö River supports high life-history diversity

comparable with previous studies in the rivers on the northern coast of Norway (Erkinaro et al. 2019; Persson et al. 2023).

Methods

Study area

The Näättämöjoki River (Neidenelva in Norwegian; Njauddám in Skolt Sámi) is a transboundary catchment between northern Finland and Norway (69°N, 29°E; Fig. 1) covers a total area of 2962 km² and is characterized by little human influence and good water quality (Niemelä et al. 2015; Kytökorpi et al. 2024). Stocking juvenile salmon or eggs reared outside the catchment area is currently prohibited by law, and the last stocking of salmon fry took place in the mid-1980s (Niemelä et al. 2015). Salmon have been detected up to 220 km upstream of the river mouth, and adult salmon are regularly caught along ca. 110 km of the mainstem and

one main tributary, Silisjoki (Vähä et al. 2008; Niemelä et al. 2015).

Samples and genotypes

We sampled 283 juveniles of 0–4 years of age by electrofishing from eight different areas across the Näättämö River for population genetic analysis (Table 1, Fig. 1). DNA from all individuals was purified from fin-clip samples using a salt extraction protocol (Aljanabi and Martinez 1997). Each sample was genotyped using a 60 K Atlantic salmon SNP array developed by the Centre for Integrative Genetics (CIGENE), Ås, Norway. To further explore the population structure of the region, we also included 1519 individuals genotyped using the same SNP array sampled from 42 locations in the Teno River (68–70° N, 25–27° E; total area of 16 386 km²) (Johansson et al. (2024); Online Resource 1, Table S1), which is separated from the Näättämö River by ca. 250 km (Vähä et al. 2008). The SNP coordinates were based on genome version GCA_905237065.2, Ssal_v3.1,

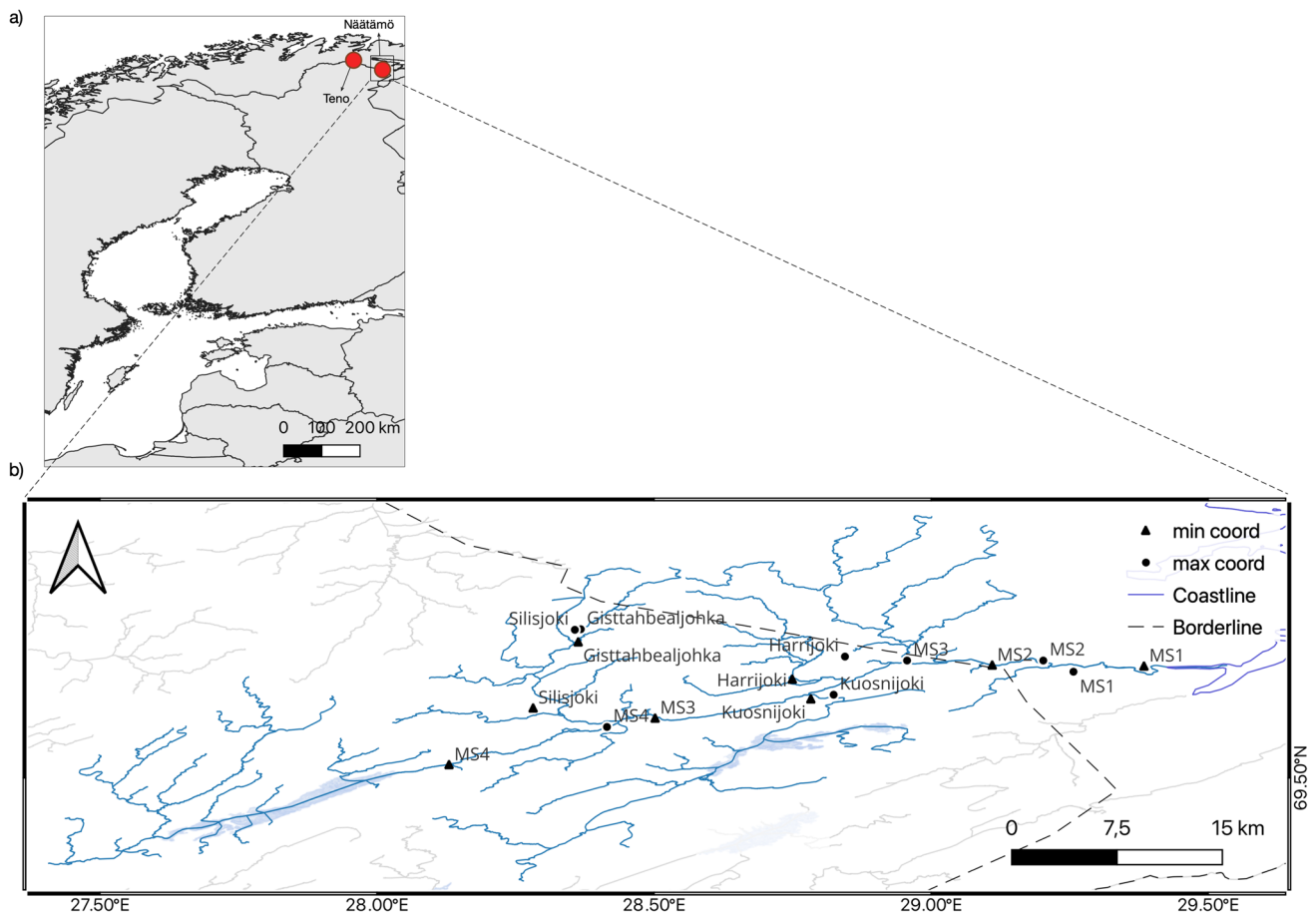


Fig. 1 a) Map of northern Europe and b) sampling locations along the Näättämö River. Minimum (triangle) and maximum (circle) X, Y coordinates for the electrofishing per sampling area

Table 1 Sampling location, number of juvenile Atlantic salmon collected and genotyped, minimum and maximum X, Y coordinates of the sampling area, year of sampling and genetic diversity (H_E , expected heterozygosity; H_O , observed heterozygosity), country and abbreviated location names for each sampling location in the Näättämö River

Name	Country	Abbre. name	#samples	X (min., max.)	Y (min., max.)	Sampling year	H_E	H_O
Gisttahbealjohka	Finland	-	17	552659, 552786	7738130, 7740647	2019	0.314	0.347
Silijoki	Finland	-	49	549798, 552375	7724753, 7740517	2019	0.341	0.345
Harrijoki	Finland	-	42	567807, 571353	7731008, 7735622	2019	0.335	0.335
Kuosnijoki	Finland	-	23	569219, 570793	7727066, 7727917	2020	0.337	0.346
Mainstem 1	Norway	MS1	30	587414, 592295	7733105, 7734478	2020	0.345	0.353
Mainstem 2	Norway	MS2	22	581689, 585223	7734288, 7735284	2019	0.34	0.35
Mainstem 3	Finland	MS3	41	558402, 575713	7722909, 7734,959	2019	0.343	0.35
Mainstem 4	Finland	MS4	54	544111, 555066	7713225, 7721004	2019	0.344	0.350

by aligning SNP probes to the genome using BWA v.0.7.17 (Li and Durbin 2009) using an in-house script.

Data filtering

Data were filtered using vcftools v0.1.16 (Danecek et al. 2011) and PLINK v1.09 (Purcell et al. 2007) according to the following criteria: (1) removing loci with more than 10% missing data (--geno 0.1), (2) removing individuals with more than 10% missing data (--mind 0.1), (3) removing loci deviating from Hardy–Weinberg equilibrium (--hwe 0.01), (4) removing loci with minor allele frequencies below 0.01 (--maf 0.01). For the population structure analysis, we (5) filtered SNPs in strong linkage disequilibrium (LD; --indep 50 5 1.5) and (6) removed potential close relatives with a PI_HAT (score of the proportion of sites in identity-by-descent IBD) > 0.5, i.e., we retained only one individual per group. Steps 3, 4, 5, and 6 were applied separately to each river (Näättämö and Teno) (details per system in Online Resource 2, Table S2). We based the HWE calculation only on individuals from the Teno mainstem (n = 146 samples, Group A = Piltamo, Sirmma, Garnjarga, and Kortsham, Online Resource 1, Table S1), which do not exhibit significant population structuring ($F_{ST} = 0.01–0.02$, Online Resource 4, Table S3).

Basic statistics, genetic diversity, population structure and migration pattern analysis

Observed and expected heterozygosities (H_O and H_E , respectively) were calculated for all sample locations using PLINK software. We calculated pairwise F_{ST} (Weir and Cockerham 1984) among sampling locations using the R package stamppFst (Pembleton et al. 2013): (i) within Näättämö, and (ii) among Näättämö and Teno rivers. To examine the genetic structure between different locations of the Näättämö and Teno Rivers, we first performed a principal component analysis (PCA) implemented in PLINK. Second, to infer the number of populations on different combinations of datasets, we used the maximum likelihood analysis of individual

ancestries by Admixture software (Alexander et al. 2009): (i) for the eight Näättämö locations, the number of ancestral populations (K) was set from 1 to 10; (ii) for locations from the mainstem (i.e., MS1, MS2, MS3, MS4) and Kuosnijoki tributary, K was set from 1 to 10; and (iii) for Näättämö and Teno datasets, K was set from 1 to 51. The optimal K value was selected based on the lowest cross-validation error and visual inspection of co-ancestry values.

We estimated the direction and magnitude of gene flow among the sampling sites between the Näättämö and Teno systems using the divMigrate() algorithm (Sundqvist et al. 2016). This method was selected due to its computational efficiency and independence on prior assumptions, although it may be sensitive to lower sample size (Sundqvist et al. 2016). We calculated the number of migrants (N_m) per generation moving between pairs of sampling areas, derived from measures of genetic diversity between populations (Sundqvist et al. 2016). Drawing on these earlier analyses of genetic structure (Online Resource 3, Fig. S2; Online Resource 4, Table S3) which depict low level of differentiation between locations of the mainstem Teno River and the Näättämö River, we focused on comparing gene flow between all Näättämö locations and the following Teno location groups: i) Upper Group A; ii) Lower Group B and iii) Middle Group C (Online Resource 1, Table S1).

Assignment analysis

We evaluated the assignment accuracy of a 180 SNP panel designed for genome stock identification (GSI) of Teno River populations (Johansson et al. 2024) for population assignment within the Näättämö River. These analyses were conducted using the R package Rubias v0.3.3 (Moran and Anderson 2018). Our evaluation involved two distinct approaches: (i) the leave-one-out approach, in which we assigned individuals from a reference dataset back to their collection site, and ii) 100% simulations, where mixtures with 100% of the individuals from one collection site were simulated. Moreover, incorporating the findings previously obtained by Admixture analysis to improve accuracy, we

redefined the reporting groups: the sites from the mainstem (i.e., MS1, MS2, MS3, MS4) and Kuosnijoki tributary, Gisttahbealjohka—Silisjoki complex and eight differentiated individuals from the Gisttahbealjohka and Silisjoki locations (details on Online Resource 2, Table S2).

Life-history strategies within the Näättämö River salmon population

A fish-scale collection comprising c. 22,000 Atlantic salmon was collected over 48 years (1975–2022) from the mainstem sections (i.e., MS1, MS2 and MS3) of the Näättämö River (Niemelä et al. 2004). Recreational tourist anglers and local fishers collected scale samples using diverse catching methods (i.e., rod 46.3%, gill nets 22.7% and cast nets 31%) during the fishing season (June—August). The life-history strategy for each sample was determined by examining the scale growth rings, which provided information about the age at which the fish left freshwater and migrated to the sea (river, RA), the number of winters they spent at sea before returning to spawn for the first time (sea age at maturity or sea winters, SW), and the possible earlier spawning events (repeat spawners). Trained experts evaluated scale growth rings following the international guidelines for Atlantic salmon scale reading (ICES 2011). Individuals without sex information, kelts i.e., adults that have recently spawned, often in poor condition (Mobley et al. 2021), and escaped salmon of aquaculture origin were excluded.

The assessment of diversity in life-history strategies was accomplished by identifying unique combinations of the number of years salmon spend in freshwater and in the ocean and the number of reproductive events. To determine the relationship between the number of documented strategies and the number of individuals sampled over 48 years, we implemented an individual-based rarefaction curve with a 95% unconditional confidence interval. Life-history strategies were ranked by frequency and the proportion of each strategy was plotted against its rank.

Results

Genetic diversity, population structure analysis

After quality control, we retained 17227 SNPs and 252 individuals for the Näättämö River (Online Resource 1, Table S1 and Online Resource 2, Table S2). Observed and expected heterozygosity per sampling location ranged from 0.314–0.353 (Table 1). Little or no clustering was observed among the four mainstem sampling locations of the system (MS1, MS2, MS3 and MS4) and Kuosnijoki tributary, which formed a single cluster based on principal component

analysis (PCA; Fig. 2a). The other tributaries formed two distinct clusters: i) Gisttahbealjohka – Silisjoki complex (largest tributary of the river) and ii) Harrijoki (Fig. 2a). In agreement with the PCA results, Admixture analysis revealed that the expected number of ancestral populations (K value) was three (Fig. 2c; Online Resource 3, Fig. S1). Eight individuals with over 99% ancestry in common with each other were found in the Gisttahbealjohka (4 individuals) and Silisjoki (4 individuals) from an unknown population (Details in Online Resource 2, Table S2). For the four locations belonging to the mainstem and Kuosnijoki tributary, $K=1$ was found, further supporting the lack of a structure between these locations. Genetic differentiation (F_{ST} , Weir and Cockerham mean) for the Näättämö River was low among the four mainstem sites and Kuosnijoki tributary (F_{ST} ranging from 0.001–0.009), while the three remaining tributaries had slightly higher levels of differentiation (F_{ST} ranging from 0.016–0.035) (Fig. 2b).

We incorporated SNP data from the neighbouring Teno River to delve deeper into the population structure of the region. Following quality control, we kept we keep 12912 SNPs in common and 1651 samples (1399 Teno; 252 Näättämö) (details per system are provided in Online Resource 2, Table S2). Observed and expected heterozygosity per sampling location ranged from 0.257–0.349 (details per system are provided in Online Resource 1, Table S1). PCA of the combined samples revealed that the Näättämö salmon clustered within Teno River samples (Details in Online Resource 3, Fig. S2). Admixture predicted that the best number of clusters was 23 (Online Resource 3, Fig. S3). F_{ST} values between the Näättämö and Teno River samples ranged from 0.013 to 0.132. The higher F_{ST} values were observed between the Näättämö River and Teno tributaries ($F_{ST}=0.045–0.132$), while the sections with lower differentiation were mainly located between Näättämö River and Teno mainstem locations ($F_{ST}=0.013–0.034$) (see Online Resource 4, Table S3). Gene flow was observed among samples collected from all analyzed locations in both the Näättämö and Teno Rivers (Online Resource 5, Table S4). The gene flow was higher within the Näättämö ($N_m=0.37–1$) and Teno River ($N_m=0.82–1$) than between the rivers ($N_m=0.30–0.59$), excluding Gisttahbealjohka tributary. No significant asymmetric gene flow ($P>0.05$) was detected between any pair of sampling locations. Notably, Gisttahbealjohka showed lower N_m values, which could be attributed to the smaller sample size.

Assignment analysis

From the panel of Johansson et al. (In press) designed for Teno River, we found 179 out of 180 SNPs. The mean assignment accuracy to sampling locations for the SNP panel were 44% and 47% for the leave-one-out and 100%

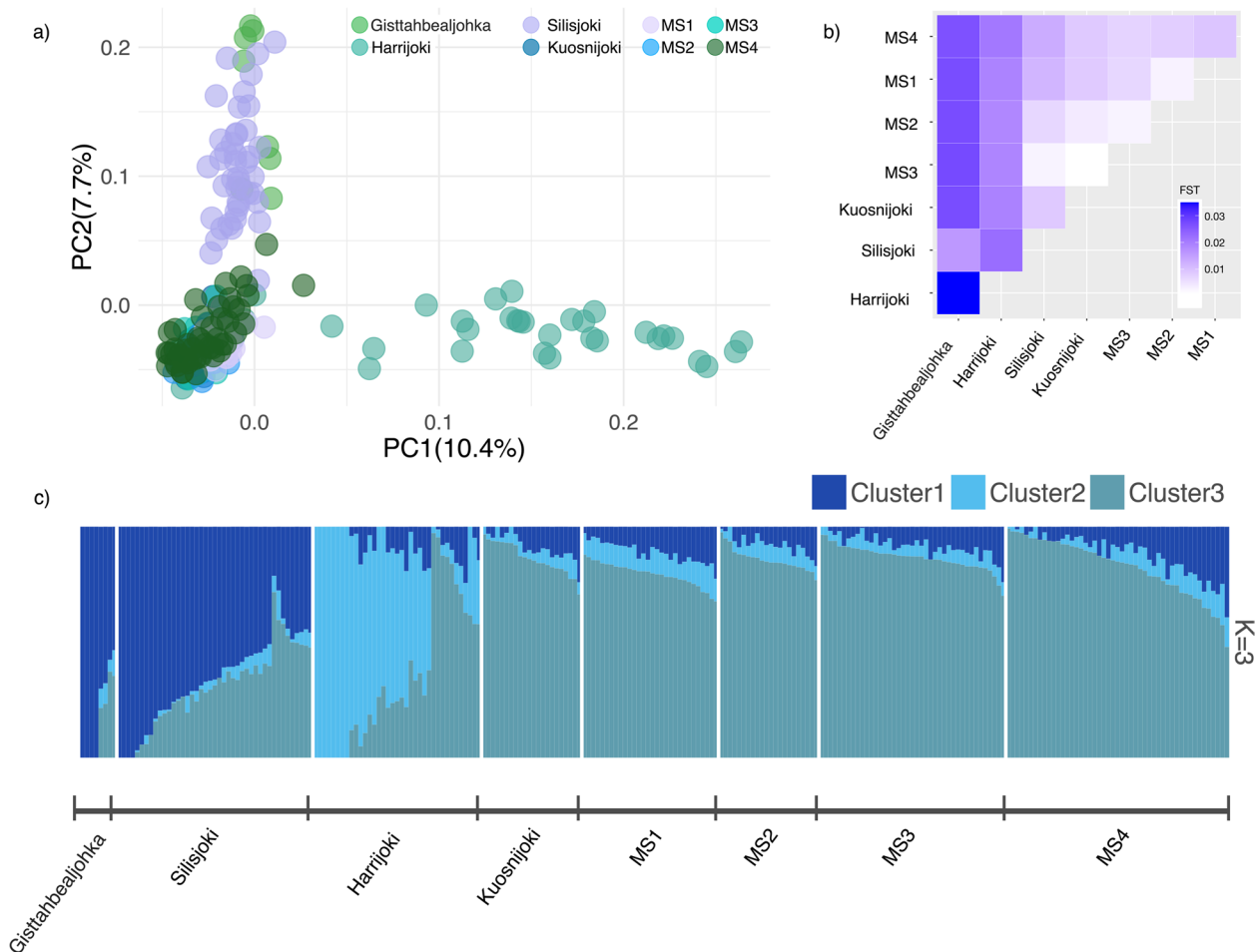


Fig. 2 a) Principal Component Analysis (PCA) of 252 juvenile Atlantic salmon samples from the Näättämö River. Each sampling location had a unique color. The X- and Y-axis titles show the percentage variation explained by PC1 and PC2, respectively; b) Pairwise F_{ST} values between the eight sampling locations from the Näättämö River; c)

Admixture results for three genetic clusters ($K=3$) for the Näättämö dataset. Each column represents an individual ordered by sampling location, indicated on the x-axis. The sampling location abbreviations are listed in Table 1

simulation approaches, respectively (Table 2). In contrast, when defining the three reporting groups based on the Admixture results, notably higher accuracy was observed, with mean accuracies of 85% and 82% for the leave-one-out and 100% simulation approaches, respectively.

Life-history strategies

Based on almost 18000 samples, we identified 59 distinct life-history strategies, including various combinations of river ages from 1 to 7 years, sea ages prior to first spawning from 1 to 4 years, and numerous types of repeat spawners (Fig. 3a). Of these, 23 strategies correspond to salmon caught during their first return to spawn, representing most individuals (95.6%). The remaining 4.4% were repeat spawners, but they displayed 36 different life-history strategies, accounting for 61% of the total life-history variation

(54.6% in males; 45.4% in females). Among those individuals categorized as repeat spawners, 98.4% were alternate spawners (i.e., salmon returning to spawn two or more years after their first spawning event), spanning 28 distinct strategies. In contrast, only 1.6% were consecutive spawners (i.e., salmon returning to spawn the year following their first spawning event), spanning eight strategies.

One-quarter of all the analyzed life-history strategies (16 out of 59) were observed only once, whereas the five most common strategies comprised 77.3% of all individuals. The predominant strategies in the system were: 4–1 (river age – sea age; 30.9% of individuals), 4–2 (15.0%), 3–1 (12.8%), 5–1 (10.4%) and 4–3 (8.4%). The sea ages composition of the river corresponded to 54.9% of individuals classified as 1SW, 25.4% as 2SW, 14.9% as 3SW, 0.3% as 4SW and 4.4% as repeat spawners. The most common river ages in the Näättämö system were 4 (57%) and 3 (23.4%) individuals.

Table 2 Assignment accuracy for eight populations from the Näättämö River using 179 SNP panel described in Johansson et al. (In press)

Reporting group	Sampling location		Sampling location + genetic inf	
	Leave-one-out	100% simulations	Leave-one-out	100% simulations
Gisttahbealjohka	25%	37%	79%	71%
Silisjoki	67%	83%		
Harrijoki	68%	71%	70%	86%
Kuosnijoki	14%	7%	91%	97%
MS1	37%	53%		
MS2	9%	6%		
MS3	42%	56%		
MS4	47%	66%		
NAPOP	-	-	75%	74%
	44%	47%	85%	82%

“NAPOP” indicates samples clustered by admixture from an unknown population

Return timing also varied by life-history strategy and sex. Between 1975 and 2022, most fish caught early in the fishing season (weeks 22–24) were 2SW and 3SW females, whereas 1SW males predominantly returned later (weeks 25–35; Online Resource 6, Fig. S4). The oldest salmon recorded in the system was a 13 years old female (106 cm, 12 kg) caught in July 1975. Its life history was 5-2S3S1:

5 years in the river, 2 years at sea, a first spawning migration, followed by 3 full years at sea, and a second spawning migration before being caught during its third spawning migration in the river.

The rarefaction curve did not reach an asymptote (Fig. 3b), suggesting the possibility of discovering additional rare strategies with an increased sample size. Our analyses

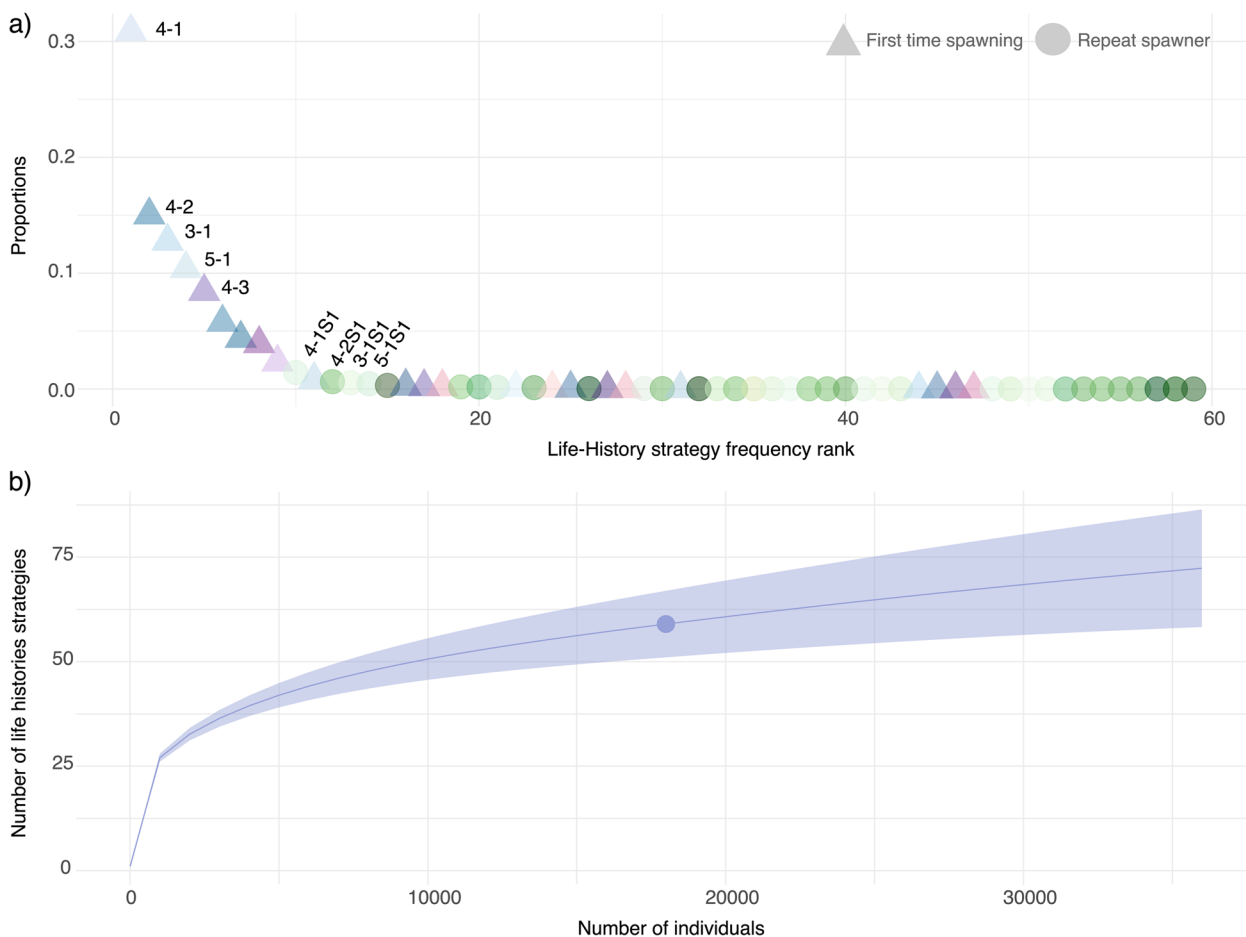


Fig. 3 Life-history strategies composition along the Näättämö River. **a)** The proportion of each life-history strategy observed in the Näättämö River ranked by their frequency in catches (triangles: first time spawning strategies; circles: repeat spawning strategies). **b)** Rarefaction

curve of the number of life-history strategies for the 48-year sampling period with the shaded area representing 95% unconditional confidence interval

of rarefaction and extrapolation curves did not reveal any changes in the richness of life-history strategies throughout the analyzed period (Online Resource 6, Fig. S5).

Discussion

Low genetic differentiation within the Näättämö river

Along the mainstem locations (M1, M2, M3 and M4) and the Kuosnijoki tributary, weak or no genetic structure, minimal levels of differentiation and high gene flow were observed, consistent with natural straying within the system. Whereas the other tributaries formed two distinct clusters, i.e., Gisttahbealjohka—Silisjoki complex and Harrijoki tributary, characterized by low levels of differentiation. Similar patterns of low genetic divergence within rivers have been found in other systems that hold wild Atlantic salmon populations (Primmer et al. 2006; Dionne et al. 2009; Wellband et al. 2019; Östergren et al. 2021). Some previous studies have suggested the implications of straying from hatchery or aquaculture-reared salmon. However, in the case of the Näättämö River, the introduction of salmon from outside of the catchment area was prohibited by law in the late 1980s (Niemelä et al. 2001). Prior to this prohibition, only small numbers of mostly locally derived hatchery-reared fry had been stocked in several locations (Niemelä et al. 2001, 2015). While it seems unlikely that this would have had a major effect on the current genetic structuring within the system, its effect cannot be completely ruled out. We were unable to address this question directly, as no hatchery-origin salmon samples were available for comparison. Therefore, further investigation is warranted. Another potential factor affecting genetic structuring is the reproduction of escaped farmed Atlantic salmon over the system. However, an extensive monitoring program of 25 years from 1989 to 2013 showed a low incidence of escaped farmed salmon (mean incidence 0–0.04) (Diserud et al. 2019), which indicates a low risk of genetic change (<4% incidence) (Taranger et al. 2015).

Between-river migration or straying can also contribute to the weak genetic structure within the Näättämö River. The nearest river with comparable genomic data was the well-studied Teno River (Niemelä et al. 2004; Erkinaro et al. 2019). Salmon originating from the Teno River have been caught over 600 km along the North-Norwegian coast (Svenning et al. 2019), depicting their wide dispersal potential. Upon comparing both systems, we found low levels of genetic differentiation mainly between the mainstem sections, with high bidirectional gene flow. Notably, we observed that the levels of genetic differentiation between the Näättämö River and Teno mainstem were lower ($F_{ST}=0.013–0.019$) than

some within-Teno comparison, where F_{ST} values ranged from 0.013 to 0.119 (see Online Resource 4, Table S3). Earlier studies using microsatellite loci have shown that the Näättämö system has clustered with other rivers of the Barents Sea area, including the Teno River (Zueva et al. 2018, 2020). In contrast, Vähä et al. (2008) reported Näättämö as a distinct genetic group using 29 microsatellites, and although the mean gene flow between Näättämö and Teno was low, it remained comparable to within-Teno estimates. The discrepancy with our results potentially arises from the higher-resolution markers and larger sample size from our study, allowing us to detect subtle patterns of gene flow and previously unresolved structure. Taken together, we suggest that the low genetic differentiation and weak structure observed within Näättämö River may have been influenced by natural straying within the system and potentially other adjacent systems to the Näättämö River, such as the Teno River.

Performance of a 180 SNP panel for genetic stock identification

Genetic stock identification (GSI) has been widely used for Atlantic salmon across a broad geographical coverage (Gilbey et al. 2018; O'Sullivan et al. 2022; Ozerov et al. 2017; Svenning et al. 2019), whereas the use of the GSI in within-river analyses is limited (Primmer et al. 2016; Vähä et al. 2007; 2017). By exclusively considering the sampling locations, we observed that sites exhibiting slightly higher genetic divergence, specifically tributary locations (Silisjoki and Harrijoki), showed better accuracy (67–68%) than those locations from the mainstem system (9–47%). One factor that can influence GSI success is the level of genetic differentiation between stocks (Vähä et al. 2017). For example, the Snake River basin's steelhead trout (*O. mykiss*) exhibited reduced GSI accuracy due to low genetic differentiation among populations resulting from translocation (Powell and Campbell 2020). Incorporating the genetic structure information, i.e., grouping as three independent reporting groups those sites from i) the mainstem and Kuosnijoki tributary, ii) Gisttahbealjohka and Silisjoki complex and iii) eight samples from unknown origin the from the Gisttahbealjohka and Silisjoki rivers, significantly enhanced assignment success. Particularly for the group composed by the mainstem and Kuosnijoki tributary (91%) and Gisttahbealjohka—Silisjoki complex (76%). Vähä et al. (2017) also noted that less distinct populations required larger sample sizes than more diverged populations (optimal: $n > 100$, $F_{ST} > 0.07$; $n > 200$, less diverged). The mean sample size per location in our system was 32, with a range of 8–49, which probably influenced the mean assignment accuracy to sampling locations results that improved by incorporating the genetic information. Therefore, the SNP panel initially developed for the

Teno River (Johansson et al. 2024) performed reasonably well for GSI in the Näätämö River. Nevertheless, selecting more informative SNPs specifically for this system, increasing the sample size (e.g., Gisttahbealjohka) or including additional populations (Kallojoki and Vuosttamušjohka tributaries) may substantially enhance the GSI accuracy.

Exploring life-history strategies along the system

Previous studies have shown that Atlantic salmon display a broad range of life-history strategies. For example, research on the Pechora River in Russia revealed 24 distinct strategies (Studenov et al. 2008), whereas studies on 179 Norwegian rivers identified 141 distinct strategies, ranging from 1 to 51 per river (Persson et al. 2023). Exceptional cases include the Teno River, in which 121 strategies have been documented for a single system (Erkinaro et al. 2019). The Näätämö salmon population displayed a wide spectrum of life-history strategies, represented by 59 unique strategies, the second highest reported for a single river. The five most frequent strategies identified in our system (i.e., river age—sea age; 4–1, 4–2, 3–1, 5–1, and 4–3) align with the same categories observed in the Teno system, encompassing 79% of the individuals sampled in Erkinaro et al. (2019), and 77% for the Näätämö system.

Our results also revealed slight changes to the sea-age composition of Näätämö River salmon previously reported for 1975 to 2003 (Niemelä et al. 2004) with reductions in 1SW and 3SW proportions (from 62 to 55% and 16% to 15%, respectively) and increases in 2SW and repeat spawners proportions (from 19 to 25% and 3.0% to 4.4%, respectively). A consistent large-scale phenomenon has been observed in some northern rivers, characterized by a transition in salmon populations from 1 to 2SW fish, which has been partly attributed to the ban of drift nets on the Norwegian coast in late 1989 and the increased sea surface temperature (Otero et al. 2012; Erkinaro et al. 2019; Harvey et al. 2021; Vollset et al. 2022). Further analysis is necessary to determine if the Näätämö River exhibits this same shift pattern. The general predominance of first-time spawning salmon compared to repeat spawners remained consistent, albeit with a slight decrease of approximately 1% in first-time spawners.

Repeat spawners play an important role in population dynamics (Persson et al. 2023). Research has shown that even small proportions of repeat spawners can act as a buffer during periods of low abundance of first-time spawners (Bordeleau et al. 2020). On average during these periods, repeat spawning females contributed approximately 18.2–35.3% of all the eggs produced by the populations (Bordeleau et al. 2020). Furthermore, repeat spawners may provide a valuable source of genetic diversity by simultaneously

increasing the number of cohorts spawning (Erkinaro et al. 2019; Mobley et al. 2024). By spawning multiple times, they can buffer against unpredictable events that threaten population recruitment (Reid and Chaput 2012; Harvey et al. 2021). In less predictable environments, repeat spawning individuals may introduce favorable traits into the gene pool, as those that successfully spawn more than once potentially possess beneficial traits for survival and reproduction, which they pass on to their progeny, thereby contributing to the sustainability and stability of the population over time (Aykanat et al. 2019; Birnie-Gauvin et al. 2019). In the Näätämö River, there was a high level of variation in the specific life-history strategy among the repeat spawners, comprising 61% (36 of 59) of the total life-history strategies observed in the river, despite constituting only 4% of the total frequency of individuals. Our findings are consistent with previous research on the Teno River, which revealed that 76% of the variation in life-history strategies (91 of 120 observed strategies) is attributable to repeat spawners (Erkinaro et al. 2019). Similarly, in 170 Norwegian rivers, 75% of the variation was attributable to repeat spawners (106 from 141 observed strategies) despite their low total frequency (4%) (Persson et al. 2023). Alternate spawners were the predominant strategy in our system, which is consistent with previous studies that have suggested that this strategy is most common in more northern latitudes, while consecutive spawning is more prevalent in southern latitudes (Niemelä et al. 2006; Chaput and Benoit 2012; Reid and Chaput 2012; Erkinaro et al. 2019; Kaland et al. 2023).

Management implications and future work

Given the recent decline in the abundance of the Näätämö salmon stocks and the rapid pace of environmental change, it would be important to revise the current management framework. This framework, based on a bilateral fishing agreement between Finland and Norway dating back to the 1970s–1980s, is complex and slow, hampering swift conservation efforts (Kytökorpi et al. 2024). To address these challenges, an adaptive management approach, informed by up-to-date knowledge of stock status, should be implemented to enable quick and flexible reactions to changes in population status and structure of the Näätämö salmon, and the challenges posed by the rapid environmental changes, such as the ongoing dramatic increase in invasive pink salmon (*Oncorhynchus gorbuscha*) populations (Staveley et al. 2025).

As part of this adaptive framework, the effective conservation and management of the Näätämö salmon stocks requires systematically monitored genetic structure, genetic diversity, and life-history variation as part of cross-border

collaboration. Our findings indicate weak genetic differentiation across the mainstem locations and Kuosnijoki tributary, supporting the idea of managing these areas as a single unit. However, we have observed some level of genetic differentiation in the Silisjoki-Gisttahbealjohka complex and Harrijoki tributaries that should not be overlooked and warrants special attention. Specifically, one of the main purposes of the monitoring should be to enhance the resolution of the baseline genetic structure. For instance, it would be advisable to include additional samples from the Gisttahbealjohka tributary, given the low sample size retained after quality control (i.e., $n=8$, of which half belong to an unknown population). Additionally, expanding the baseline by incorporating previously unsampled areas, such as the Kallajoki and Vuosttamušjohka tributaries, where considerable juvenile production still occurs despite the reduced discharge caused by water diversion to the Gandvik hydro-power facility (Niemelä et al. 2015; Orell et al. 2024). This would provide a more comprehensive understanding of population structure across the Näättämö River. Moreover, substantial gene flow within the Näättämö River may promote demographic and genetic rescue effects, maintaining overall population persistence and resilience in the face of environmental change (Garant et al. 2007; Whiteley et al. 2015). Thus, maintaining connectivity across habitats should therefore be a conservation priority.

Despite the weak genetic structure observed within the Näättämö River, we cannot exclude the possibility of there being life-history differentiation among the genetic clusters (i.e., mainstem locations-Kuosnijoki tributary, the Gisttahbealjohka-Silisjoki tributaries and the Harrijoki tributary). In this study, we were not able to address this question because phenotypic data were only available for individuals from the mainstem section, so further investigation is warranted. Nonetheless, we observed an overall high diversity of life-history strategies, exhibiting the second-highest number reported for a single river. Intraspecific variation in traits such as age at maturity and migration timing plays a crucial role in enhancing resilience to environmental change, stabilizing populations and supporting sustainable harvest (Hilborn et al. 2003; Östergren and Nilsson 2012; Gharrett et al. 2013; Miettinen et al. 2021; Carvalho et al. 2023). Preserving this diversity is therefore essential for the long-term viability of the Näättämö salmon stocks. Including targeted measures, such as regulating the early-season fishery, could help safeguard specific salmon life histories (Erkinaro et al. 2019). The fishing season on the Näättämö River begins in early June, making it one of the earliest in Northern Norway (Kytökorpi et al. 2024). Early-season fisheries primarily target 2–4SW salmon and repeat spawners (Online Resource 6, Fig. S4), which primarily consist of large, high-fecundity females (Niemelä et al. 2006) that play a crucial role in population productivity.

Finally, salmon life-history variation—particularly sea age—has been associated with large-effect loci (Barson et al. 2015; Sinclair-Waters et al. 2020), offering promising avenues for population monitoring and conservation (Waples et al. 2022). We recommend assessing the adaptive potential of the Näättämö stocks, and more broadly of Atlantic salmon populations, in response to human induced selection, by monitoring changes of allele frequencies of large-effect loci associated with key life-history traits over time.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10592-025-01717-y>.

Acknowledgements We would like to thank sample providers (Natural Resources Institute Finland staff, traditional and recreational fishers), scale age readers and the genetics laboratory team (Helena Johansson, Iikki Donner and Annukka Ruokolainen) for their assistance. We acknowledge the DNA Sequencing and Genomics Laboratory at the University of Helsinki (Institute of Biotechnology; supported by HiLIFE and Biocenter Finland funding) and CIGENE (Centre of Integrative Genetics, Norwegian University of Life Sciences, Norway) for sequencing. CSC (IT Center for Sciences, Finland) for access to computational resources.

Author contributions Conceptualization: VLP, CRP, MIC, MSW; Sample collection: JE, PO; Data curation and analysis: MIC, MSW, JE, PO; Visualization: MIC, ASL, AL, MF; Funding acquisition: CRP, VLP; Writing-original draft: MIC; Writing-review & editing: All authors.

Funding Open Access funding provided by University of Helsinki (including Helsinki University Central Hospital). Funded by the University of Helsinki, Natural Resources Institute Finland (Luke) (until 2015: Finnish Game and Fisheries Research, Institute), Ministry of Agriculture and Forestry (Finland), Neiden Fiskefelleskap and Norwegian Environment Agency and the European Union (ERC, FishLEGs, 101054307). Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council Executive Agency. Neither the European Union nor the granting authority can be held responsible for them.

Data availability Data for this study are available at Zenodo: <https://doi.org/10.5281/zenodo.16762360>.

Declarations

Ethical approval This study used Atlantic salmon tissue samples collected from an fisheries monitoring programs. All sample collection complied with applicable national legislation of Finland and Norway.

Consent for publication All authors consent to submitting this article to *Conservation Genetics*.

Conflicts of interest/Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format,

as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Agashe D (2009) The stabilizing effect of intraspecific genetic variation on population dynamics in novel and ancestral habitats. *Am Nat* 174:255–267. <https://doi.org/10.1086/600085>
- Alexander DH, Novembre J, Lange KF (2009) Fast model-based estimation of ancestry in unrelated individuals. *Genome Res* 19:1655–1664. <https://doi.org/10.1101/gr.094052.109>
- Aljanabi S, Martinez I (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR- based techniques. *Nucleic Acids Res* 25:4692–4693. <https://doi.org/10.1093/nar/25.22.4692>
- Andreassen R, Hagen-Larsen H, Sánchez-Ramos I et al (2008) STR and bi-allelic polymorphisms in Atlantic salmon: Tools for tracing large scale escapees from salmon farms. *Forensic Sci Int Genet Suppl Ser* 1:586–588. <https://doi.org/10.1016/j.fsigss.2007.10.078>
- Asplund T, Veselov A, Primmer CR, et al (2004) Geographical structure and postglacial history of mtDNA haplotype variation in Atlantic salmon (*Salmo salar* L.) among rivers of the White and Barents Sea basins. *Ann Zool Fennici* 41: 465–475. <https://www.jstor.org/stable/23736160>
- Aykanat T, Johnston SE, Orell P et al (2015) Low but significant genetic differentiation underlies biologically meaningful phenotypic divergence in a large Atlantic salmon population. *Mol Ecol* 24:5158–5174. <https://doi.org/10.1111/mec.13383>
- Aykanat T, Ozerov M, Vähä JP et al (2019) Co-inheritance of sea age at maturity and iteroparity in the Atlantic salmon *vgl13* genomic region. *J Evol Biol* 32:343–355. <https://doi.org/10.1111/jeb.13418>
- Barson NJ, Aykanat T, Hindar K et al (2015) Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature* 528:405–408. <https://doi.org/10.1038/nature16062>
- Besnier F, Glover KA, Skaala O (2011) Investigating genetic change in wild populations: Modelling gene flow from farm escapees. *Aquac Environ Interact* 2:75–86. <https://doi.org/10.3354/aei00032>
- Birnie-Gauvin K, Thorstad EB, Aarestrup K (2019) Overlooked aspects of the *Salmo salar* and *Salmo trutta* life cycles. *Rev Fish Biol Fish* 29:749–766
- Bordeleau X, Pardo SA, Chaput G et al (2020) Spatio-temporal trends in the importance of iteroparity across Atlantic salmon populations of the northwest Atlantic. *ICES J Mar Sci* 77:326–344. <https://doi.org/10.1093/icesjms/fsz188>
- Carvalho PG, Satterthwaite WH, O'Farrell MR et al (2023) Role of maturation and mortality in portfolio effects and climate resilience. *Can J Fish Aquat Sci* 80:924–941. <https://doi.org/10.1139/cjfas-2022-0171>
- Chaput G, Benoît HP (2012) Evidence for bottom-up trophic effects on return rates to a second spawning for Atlantic salmon (*Salmo salar*) from the Miramichi River, Canada. *ICES J Mar Sci* 69:1656–1667. <https://doi.org/10.1093/icesjms/fss055>
- Dadswell M, Spares A, Reader J et al (2022) The decline and impending collapse of the Atlantic salmon (*Salmo salar*) population in the north Atlantic ocean: a review of possible causes. *Rev Fish Sci Aquac* 30:215–258
- Danecek P, Auton A, Abecasis G et al (2011) The variant call format and VCFtools. *Bioinformatics* 27:2156–2158. <https://doi.org/10.1093/bioinformatics/btr330>
- Des Roches S, Post DM, Turley NE et al (2018) The ecological importance of intraspecific variation. *Nat Ecol Evol* 2:57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- Des Roches S, Pendleton LH, Shapiro B, Palkovacs EP (2021) Conserving intraspecific variation for nature's contributions to people. *Nat Ecol Evol* 5:574–582
- Dionne M, Caron F, Dodson JJ, Bernatchez L (2009) Comparative survey of within-river genetic structure in Atlantic salmon; relevance for management and conservation. *Conserv Genet* 10:869–879. <https://doi.org/10.1007/s10592-008-9647-5>
- Diserud OH, Fiske P, Særgrov H et al (2019) Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013. *ICES J Mar Sci* 76:1140–1150
- Elo K (1993) Gene flow and conservation of genetic variation in anadromous Atlantic salmon (*Salmo salar*). *Hereditas* 119:149–159. <https://doi.org/10.1111/j.1601-5223.1993.00149.x>
- Elo K, Vuorinen JA, Niemelä E (1994) Genetic resources of Atlantic salmon (*Salmo salar* L.) in Teno and Näätämö Rivers. *Northernmost Eur Hereditas* 120:19–28. <https://doi.org/10.1111/j.1601-5223.1994.00019.x>
- Ensing D, Crozier WW, Boylan P et al (2013) An analysis of genetic stock identification on a small geographical scale using microsatellite markers, and its application in the management of a mixed-stock fishery for Atlantic salmon *Salmo salar* in Ireland. *J Fish Biol* 82:2080–2094. <https://doi.org/10.1111/jfb.12139>
- Erkinaro J, Czorzlich Y, Orell P et al (2019) Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. *Can J Fish Aquat Sci* 76:42–55. <https://doi.org/10.1139/cjfas-2017-0343>
- Garant D, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct Ecol* 21:434–443
- Gharrett AJ, Joyce J, Smoker WW (2013) Fine-scale temporal adaptation within a salmonid population: mechanism and consequences. *Mol Ecol* 22:4457–4469. <https://doi.org/10.1111/mec.12400>
- Gilbey J, Coughlan J, Wennevik V et al (2018) A microsatellite baseline for genetic stock identification of European Atlantic salmon (*Salmo salar* L.). *ICES J Mar Sci* 75:662–674. <https://doi.org/10.1093/icesjms/fsx184>
- Glover KA, Skilbrei OT, Skaala Ø (2008) Genetic assignment identifies farm of origin for Atlantic salmon *Salmo salar* escapees in a Norwegian fjord. *ICES J Mar Sci* 65:921–920
- Glover KA, Pertoldi C, Besnier F et al (2013) Atlantic salmon populations invaded by farmed escapees: Quantifying genetic introgression with a Bayesian approach and SNPs. *BMC Genet* 14:14–74. <https://doi.org/10.1186/1471-2156-14-74>
- Harvey A, Skaala Ø, Borgstrøm R et al (2021) Time series covering up to four decades reveals major changes and drivers of marine growth and proportion of repeat spawners in an Atlantic salmon population. *Ecol Evol* 12:8480. <https://doi.org/10.1002/ece3.8780>
- Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. U. S. A.* 100 (11): 6564–6568. <https://doi.org/10.1073/pnas.1037274100>
- Hoban S, Bruford M, D'Urban Jackson J et al (2020) Genetic diversity targets and indicators in the CBD post-2020 global biodiversity framework must be improved. *Biol Conserv* 248:108654. <https://doi.org/10.1016/j.biocon.2020.108654>

- Hvilsom C, Segelbacher G, Ekblom R, et al (2022) Selecting species and populations for monitoring of genetic diversity. Gland, Switzerland
- ICES (2011) Report of the Workshop on Age Determination of Salmon (WKADS). ICES Expert Group reports (until 2018)
- ICES (2025) Working Group on North Atlantic Salmon (WGNAS). ICES Scientific Reports. 7(44):435 <https://doi.org/10.17895/ices.pub.28777226>
- Johansson H, Erkinaro J, Morten F et al (In press) A single nucleotide polymorphism genotyping panel for efficient genetic stock identification of the Teno river Atlantic salmon (*Salmo salar*) population complex. J Fish Biol
- Kaland H, Harvey AC, Skaala Ø et al (2023) DNA and scale reading to identify repeat spawning in Atlantic salmon: Unique insights into patterns of iteroparity. Evol Appl 16:1921–1936. <https://doi.org/10.1111/eva.13612>
- Klemetsen A, Amundsen PA, Dempson JB et al (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. Ecol Freshw Fish 12:1–59. <https://doi.org/10.1034/j.1600-0633.2003.00010.x>
- Kytökorpi M, Tynkkynen R, Kylmäaho M, et al (2024) Näätämojen lohikannan tila: Nousulohimäärät, lohisaaliit ja poikastiheydet. Luonnon- vara- ja biotalouden tutkimus 81/2024. Helsinki
- Laikre L, Hoban S, Bruford MW et al (2020) Post-2020 goals overlook genetic diversity. Science 367:1083–1085. <https://doi.org/10.1126/science.abb2748>
- Leigh DM, Hendry AP, Vázquez-Domínguez E, Friesen VL (2019) Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. Evol Appl 12:1505–1512
- Li H, Durbin R (2009) Fast and accurate short read alignment with Burrows – Wheeler transform. Bioinformatics 25:1754–1760. <https://doi.org/10.1093/bioinformatics/btp324>
- Miettinen A, Palm S, Dannewitz J et al (2021) A large wild salmon stock shows genetic and life history differentiation within, but not between, rivers. Conserv Genet 22:35–51. <https://doi.org/10.1007/s10592-020-01317-y>
- Mimura M, Yahara T, Faith DP et al (2017) Understanding and monitoring the consequences of human impacts on intraspecific variation. Evol Appl 10:121–139
- Mobley KB, Aykanat T, Czorlich Y et al (2021) Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes. Rev Fish Biol Fish 31:523–571
- Mobley KB, Barton HJ, Ellmén M et al (2024) Sex-specific overdominance at the maturation *vgl3* gene for reproductive fitness in wild Atlantic salmon. Mol Ecol 33:17435. <https://doi.org/10.1111/mec.17435>
- Moran BM, Anderson EC (2018) Bayesian inference from the conditional genetic stock identification model. Can J Fish Aquat Sci 76:551–560
- Nielsen EE, Cariani A, Mac AE et al (2012) Gene-associated markers provide tools for tackling illegal fishing and false eco-certification. Nat Commun 3:1845. <https://doi.org/10.1038/ncomms1845>
- Niemelä E, Erkinaro J, Julkunen M et al (2006) Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. J Fish Biol 68:1222–1240. <https://doi.org/10.1111/j.1095-8649.2006.01012.x>
- Niemelä E, Erkinaro J, Kylmäaho M, et al (2001) Näätämojen lohien poikastiheys ja kasvu. Helsinki, Finland
- Niemelä E, Erkinaro J, Dempson JB et al (2004) Temporal synchrony and variation in abundance of Atlantic salmon (*Salmo salar*) in two subarctic Barents Sea rivers: influence of oceanic conditions. Can J Fish Aquat Sci. <https://doi.org/10.1139/f04-208>
- Niemelä E, Länsman M, Hassinen E, et al (2015) Näätämojen moninaiskäyttösuunnitelma, osa I: Näätämojen ympäristöolosuhteet, lohien ekologia, Näätämon lohien vaellus ja saaliin ajoittuminen meressä ja joessa sekä Varanginvuonon lohienkalastuksen erityispiirteitä. Helsinki
- O’sullivan RJ, Ozerov M, Bolstad GH et al (2022) Genetic stock identification reveals greater use of an oceanic feeding ground around the Faroe Islands by multi-sea winter Atlantic salmon, with variation in use across reporting groups. ICES J Mar Sci 79:2442–2452. <https://doi.org/10.1093/icesjms/fsac182>
- Orell P, Kytökorpi M, Kuusela J, et al (2024) Mapping of the River Kallojoki salmon distribution: spawning target setting. Natural Resources and Bioeconomy Studies 99/2024. Natural Resources Institute Finland. Helsinki, p 23
- Östergren J, Palm S, Gilbey J, et al (2021) A century of genetic homogenization in Baltic salmon - Evidence from archival DNA. Proc R Soc B Sci 288:20203147. <https://doi.org/10.1098/rspb.2020.3147>
- Östergren J, Nilsson J (2012) Importance of life-history and landscape characteristics for genetic structure and genetic diversity of brown trout (*Salmo trutta* L.). Ecol Freshw Fish 21:119–133. <https://doi.org/10.1111/j.1600-0633.2011.00529.x>
- Otero J, Jensen AJ, L’Abeé-Lund JH et al (2012) Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. Ecol Evol 2:2192–2203. <https://doi.org/10.1002/ece3.337>
- Ozerov M, Vähä JP, Wennevik V et al (2017) Comprehensive microsatellite baseline for genetic stock identification of Atlantic salmon (*Salmo salar* L.) in northernmost Europe. ICES J Mar Sci 74:2159–2169. <https://doi.org/10.1093/icesjms/fsx041>
- Ozerov MY, Wennevik V, Niemelä E, et al (2023) Report XXI. Genome-wide analysis of the temporal genetic variation of Atlantic salmon populations in Finnmark rivers, northern Norway. Kolarctic CBC – Project KO4178. Finland
- Palkovacs EP, Kinnison MT, Correa C et al (2012) Fates beyond traits: Ecological consequences of human-induced trait change. Evol Appl 5:183–191. <https://doi.org/10.1111/j.1752-4571.2011.00212.x>
- Parrish DL, Behnke RJ, Gephard SR, et al (1998) Why aren’t there more Atlantic salmon (*Salmo salar*)? In: Canadian Journal of Fisheries and Aquatic Sciences. National Research Council of Canada, pp 281–287
- Pelletier MC, Ebersole J, Mulvaney K et al (2020) Resilience of aquatic systems: review and management implications. Aquat Sci 82:1–44. <https://doi.org/10.1007/s00027-020-00717-z>
- Pembleton LW, Cogan NOI, Forster JW (2013) StAMPP: an R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. Mol Ecol Resour 13:946–952. <https://doi.org/10.1111/1755-0998.12129>
- Persson L, Raunsgard A, Thorstad EB et al (2023) Iteroparity and its contribution to life-history variation in Atlantic salmon. Can J Fish Aquat Sci 80:577–592. <https://doi.org/10.1139/cjfas-2022-0126>
- Powell JH, Campbell MR (2020) Contemporary genetic structure affects genetic stock identification of steelhead trout in the Snake River basin. Ecol Evol 10:10520–10531. <https://doi.org/10.1002/ece3.6708>
- Primmer CR, Koskinen MT, Piironen J (2000) The one that did not get away: individual assignment using microsatellite data detects a case of fishing competition fraud. Proc R Soc B Biol Sci 267:1699–1704. <https://doi.org/10.1098/rspb.2000.1197>
- Primmer CR, Veselov AJ, Zubchenko A et al (2006) Isolation by distance within a river system: Genetic population structuring of Atlantic salmon, *Salmo salar*, in tributaries of the Varzuga River in northwest Russia. Mol Ecol 15:653–666. <https://doi.org/10.1111/j.1365-294X.2005.02844.x>
- Pritchard VL, Erkinaro J, Kent MP et al (2015) Single nucleotide polymorphisms to discriminate different classes of hybrid between wild Atlantic salmon and aquaculture escapees. Evol Appl 9:1017–1031. <https://doi.org/10.1111/eva.12407>

- Purcell S, Neale B, Todd-Brown K et al (2007) PLINK: a toolset for whole-genome association and population-based linkage analysis. *Am J Hum Genet* 81:559–75
- Reid JE, Chaput G (2012) Spawning history influence on fecundity, egg size, and egg survival of Atlantic salmon (*Salmo salar*) from the Miramichi River, New Brunswick, Canada. *ICES J Mar Sci* 69:1678–1685. <https://doi.org/10.1093/icesjms/fss091>
- Schindler DE, Hilborn R, Chasco B et al (2010) Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612. <https://doi.org/10.1038/nature09060>
- Shaw RE, Farquharson KA, Bruford MW et al (2025) Global meta-analysis shows action is needed to halt genetic diversity loss. *Nature* 638:704–710. <https://doi.org/10.1038/s41586-024-08458-x>
- Sinclair-Waters M, Ødegård J, Korsvoll SA et al (2020) Beyond large-effect loci: Large-scale GWAS reveals a mixed large-effect and polygenic architecture for age at maturity of Atlantic salmon. *Gen Sel Evol* 52:9. <https://doi.org/10.1186/s12711-020-0529-8>
- Skaala O, Makhrov AA, Karlsen T et al (1998) Genetic comparison of salmon from the White Sea and north-western Atlantic Ocean. *J Fish Biol* 53:569–580. <https://doi.org/10.1111/j.1095-8649.1998.tb01002.x>
- Skaala Ø, Høyheim B, Glover K, Dahle G (2004) Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): allelic diversity and identification of individuals. *Aquaculture* 240:131–143. <https://doi.org/10.1016/j.aquaculture.2004.07.009>
- Skaala Ø, Taggart JB, Gunnes K (2005) Genetic differences between five major domesticated strains of Atlantic salmon and wild salmon. *J Fish Biol* 67:118–128. <https://doi.org/10.1111/j.1095-8649.2005.00843.x>
- Staveley TAB, Ahlbeck Bergendahl I, Bárðarson H, et al (2025) Status and future perspectives of pink salmon in the Nordic region. *Boreal Environ Res*. Accepted <https://doi.org/10.60910/ber2025.wt02-y377>
- Studenov II, Antonova VP, Chuksina NA, Titov SF (2008) Atlantic salmon (*Salmo salar* Linnaeus, 1758) of the Pechora River. SevPINRO, Arkhangel'sk
- Sundqvist L, Keenan K, Zackrisson M et al (2016) Directional genetic differentiation and relative migration. *Ecol Evol* 6:3461–3475. <https://doi.org/10.1002/ece3.2096>
- Svenning MA, Falkegård M, Niemelä E et al (2019) Coastal migration patterns of the four largest Barents Sea Atlantic salmon stocks inferred using genetic stock identification methods. *ICES J Mar Sci* 76:1379–1389
- Taranger GL, Karlsen Ø, Bannister RJ et al (2015) Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES J Mar Sci* 72:997–1021. <https://doi.org/10.1093/icesjms/fus132>
- Vähä J-P, Erkinaro J, Niemelä E, Primmer CR (2007) Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. *Mol Ecol* 16:2638–2654. <https://doi.org/10.1111/j.1365-294X.2007.03329.x>
- Vähä J, Erkinaro J, Niemelä E, Primmer C (2008) Temporally stable genetic structure and low migration in an Atlantic salmon population complex: implications for conservation and management. *Evol Appl* 1:137–154. <https://doi.org/10.1111/j.1752-4571.2007.00007.x>
- Vähä J, Erkinaro J, Falkegård M et al (2017) Genetic stock identification of Atlantic salmon and its evaluation in a large population complex. *Can J Fish Aquat Sci* 74:327–338. <https://doi.org/10.1139/cjfas-2015-0606>
- Vollset K, Urdal K, Utne K et al (2022) Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Sci Adv* 8:2542
- VRL Vitenskapelig råd for lakseforvaltning (2024) Status for norske laksebestander i 2024. Rapport fra Vitenskapelig råd for lakseforvaltning nr 19
- Waples RS, Ford MJ, Nichols K et al (2022) Implications of large-effect loci for conservation: a review and case study with Pacific salmon. *J Hered* 113:121–144
- Weir BS, Cockerham CC (1984) Estimating f-statistics for the analysis of population structure. *Evolution*. <https://doi.org/10.1111/j.1558-5646.1984.tb05657.x>
- Wellband K, Mérot C, Linnansaari T et al (2019) Chromosomal fusion and life history-associated genomic variation contribute to within-river local adaptation of Atlantic salmon. *Mol Ecol* 28:1439–1459. <https://doi.org/10.1111/mec.14965>
- Whiteley AR, Fitzpatrick SW, Funk WC, Tallmon DA (2015) Genetic rescue to the rescue. *Trends Ecol Evol* 30:42–49
- Zueva KJ, Lumme J, Veselov AE et al (2018) Genomic signatures of parasite-driven natural selection in north European Atlantic salmon (*Salmo salar*). *Mar Genomics* 39:26–38. <https://doi.org/10.1016/j.margen.2018.01.001>
- Zueva KJ, Lumme J, Veselov AE, et al (2020) Population genomics reveals repeated signals of adaptive divergence in the Atlantic salmon of north-eastern Europe. In: *Journal of Evolutionary Biology*. John Wiley and Sons Inc, pp 866–878

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.